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Establishment of an *in vitro* method for evaluating whitefly resistance in tomato

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An accurate and simple evaluation method is crucial for identifying whitefly resistance in tomato breeding. We developed an *in vitro* method for evaluating resistance of tomato leaves and tested this on wild and cultivated tomato varieties. We found that young leaves observed for whitefly oviposition after 8 hours provided appropriate comparative conditions. This method effectively distinguished resistance among tomato cultivars and wild species and also demonstrated significant difference in oviposition rates among leaf positions on susceptible cultivars. The *in vitro* test was as precise as *in vivo* test using intact plants and had advantages over in *vivo test*, and can be used for evaluating resistance in large populations.

Key Words: *Bemisia tabaci*, *Solanum lycopersicum*, *Solanum habrochaites*, tomato resistance, phenotypic testing, breeding.

Introduction

The whitefly, *Bemisia tabaci*, is one of the world's most serious pests of agricultural and horticultural crops (Gerling and Mayer 1996). It is native to tropical and subtropical regions but has spread rapidly around the world (Barro *et al.* 1998). Whitefly is highly polyphagous, invading a wide range of plants including more than 900 wild and cultivated species (Brown *et al.* 1995). Whiteflies damage tomato plants by feeding resulting in leaf and fruit spotting, plant debilitation, sooty mold growth on honeydew secreted by the insects, and irregular ripening of fruit (Anderson *et al.* 2005, Pappu *et al.* 2009, Schuster *et al.* 1995, 2001). The greatest economic threat is from the transmission of plant viruses, primarily begomoviruses, and one of the most damaging of these is the tomato yellow leaf curl virus (TYLCV) (Lapidot and Polston 2006, Polston and Anderson 1997, Saikia and Muniyappa 1989).

Tomato, *Solanum lycopersicum*, is one of the world's major vegetable crops. Low levels of resistance to whitefly within *S. lycopersicum* have been reported (Freitas *et al.* 2002) and considerable costs are involved in controlling the pest chemically or biologically (Bas *et al.* 1992, De Ponti *et al.* 1975, Sánchez-Peña *et al.* 2006). There is thus an urgent need for resistant cultivars. Unfortunately, breeding for whitefly resistance has been hampered by the apparent quantitative inheritance of resistance, variation in whitefly populations, and large environmental variation (De Ponti *et al.* 1975, Bas *et al.* 1992). In addition, large plant populations are required for some whitefly resistance studies and breeding programs. A simple, effective method of evaluating resistance is thus necessary for researchers and breeders.

Some tests for whitefly resistance have used cages that clip on to plant leaves (Berlinger and de Ponti 1981, Romanow *et al.* 1991) and have revealed large differences between *S. lycopersicum* and *S. habrochaites* as hosts with respect to the life history of the whitefly, including oviposition rate, and adult and juvenile survival rates (Bas *et al.* 1992). In studies of quantitative trait loci (QTL) in tomato that influenced whitefly resistance, clip-on cages have been used. Whitefly adults were put into cages and egg numbers and empty pupae were counted after four or five weeks, or eggs and dead adults were counted after 24 hours (Bonierbale *et al.* 1994, Maliepaard *et al.* 1995, Momotaz *et al.* 2010). In other studies, plants were infested with whitefly adults, and adults and eggs were counted after one month and first to fourth instars were also counted at selected leaf nodes (Muigai *et al.* 2002, 2003). These methods have been successful in screening different tomato germplasms for resistance. However, these methods have some deficiencies. Sometimes cages are too heavy to be placed around tomato leaves. Whiteflies may escape from cages or be affected by the small living space within cages. The worst feature is that these methods require considerable space and time, and are not appropriate for testing whitefly resistance in large tomato populations. Other tests for resistance to whiteflies and spider mites have been conducted using *in vitro* leaves or leaflets evaluated *in vitro*. Leaflets were detached and placed upside-down (abaxial surface oriented upwards) in a Petri dish lined with moistened filter paper. A selected number of adult females were placed on each leaflet, and then the number of eggs and live adults were recorded after 48 hours (Alba *et al.* 2009, Snyder *et al.* 1998). We evaluated this method but the results were not ideal, there was too high whitefly adult motility to testing whitefly resistance between

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different tomato plants (data was not shown). In another spider mite bioassay, leaves were detached and inserted in small vials containing water to maintain turgor (Guo *et al.* 1993). Extent of mite infestation was evaluated during the three days period following infestation. In researching the resistance of cotton genotypes to whitefly, a cylindrical cage (40 cm height × 25 cm diameter), fabricated from wood (Jindal and Dhaliwal 2009) was successfully employed. Firdaus *et al.* (2012) reported that a leaf disc test was a good *in vitro* alternative for the clip-on cage whitefly resistance screening, as shown by the high correlation between the results obtained with this test and the clip-on cage test. The result illustrated that *in vitro* methold was entirely feasible for whitefly resistance screening, but this method needs a lot of small cages and a climate room for testing whitefly resistance in large tomato population. These equipments are luxury for some researchers and breeders. In addition, the leaf disc test is a no-choice test. Compared with no-choice test, a free-choice test is more similar with the natural environment. Consequently, it was evaluated the use of flasks and cages to develop an *in vitro* method for investigating whitefly resistance of tomato leaves.

Materials and Methods

Tomato genotypes, whitefly culture and cages

The study was conducted in the glasshouse at the Institute of Vegetables and Flowers, Chinese Academy of Agricultural Sciences, Beijing, China. Five tomato genotypes, including two whitefly resistant *S. habrochaites* (LA1777 and PI134417) and three susceptible *S. lycopersicum* (cultivar 9706, ZaoFen 2 and Moneymaker) were used. The seeds of *S. lycopersicum* ('Moneymaker' variety) were obtained from Tomato Genetics Resources Center (TGRC). *S. lycopersicum* cultivars 'cultivar 9706' and 'ZaoFen 2' were obtained from the program for Fresh Tomato Breeding at the Institute of Vegetables and Flowers. Tomato plants were grown in plastic pots (15 cm height, 10 cm down diameter, 15 cm upper diameter) which were filled with nutrition soil in the summer of 2010. Temperatures were maintained at 20–28°C and photoperiod was 12 h. Plants were watered daily, and were not fertilized. The population of *B. tabaci* was obtained from the Plant Protection Laboratory at the Institute of Vegetables and Flowers and was initially cultured on cabbage. The original *B. tabaci* population (about 20 unsexed adults) was collected from cabbages planted in the greenhouse of the Beipu Demonstration Farm, Haidian district, Beijing, in 2004. The population was identified as biotype B using an mtDNA COI marker in the laboratory (Xie *et al.* 2011). The cage used for bioassays had a square base and a tapered top (60 cm height × 60 cm length × 60 cm width). It was externally supported by six flexible plastic dowels (50 cm length × 0.5 cm diameter) and four stainless steel tubes (10 cm length × 0.6 cm diameter) and was covered with 60 mesh cloth. A zipper in the front of the cage served as the door for insertion and removal of plant material. There was also a small opening through which whiteflies were introduced into the cage (Fig. 1).

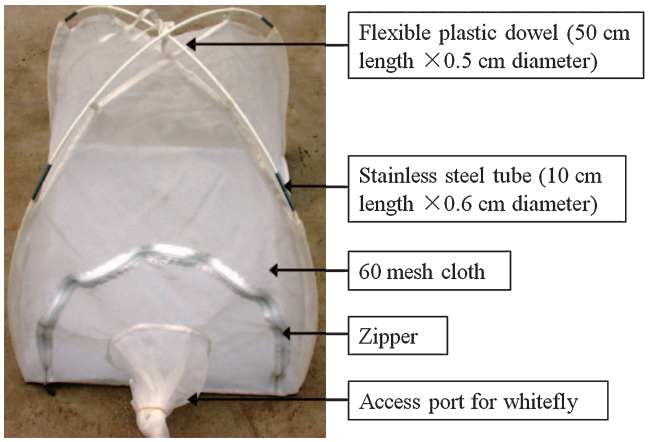

Fig. 1. The cage structure

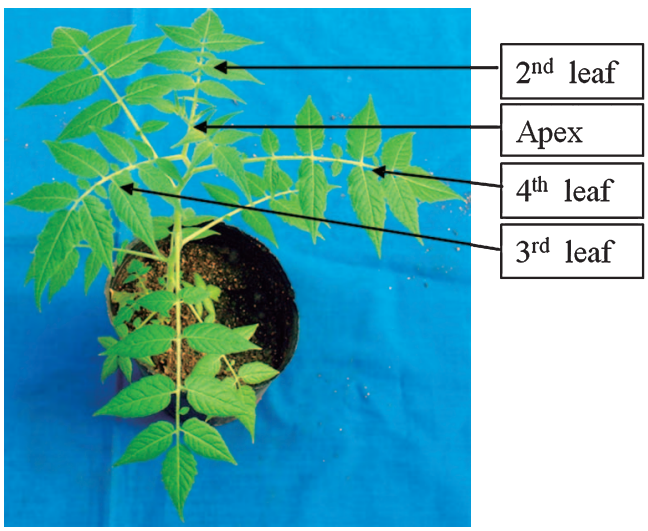

Fig. 2. Leaf position designation

Measurement of whitefly oviposition at different leaf nodes and different sampling times

An initial experiment was conducted using only the susceptible cultivated tomato cultivar 9706. Seeds were sown in plastic pots (15 cm height, 10 cm diameter, 15 cm upper diameter). These were placed inside the cages at the seedling stage to avoid any possibility of unintended infestation.

For the *in vitro* bioassays, after plants had grown six weeks, leaves from nodes 2–4, counting from the apex (Fig. 2), were cut and inserted into glass flasks filled with water and were held in place using sponge strips (Fig. 3). Twelve flasks containing leaves were placed in each split cage (four biological replications). It was also placed four intact plants (four biological replications) for *in vivo* bioassays in each cage (Fig. 3). At 08:00 a.m. about 1,200 (×8) *B. tabaci* adults (~100 per leaf) were randomly collected from the cabbage culture, and released into each cage.

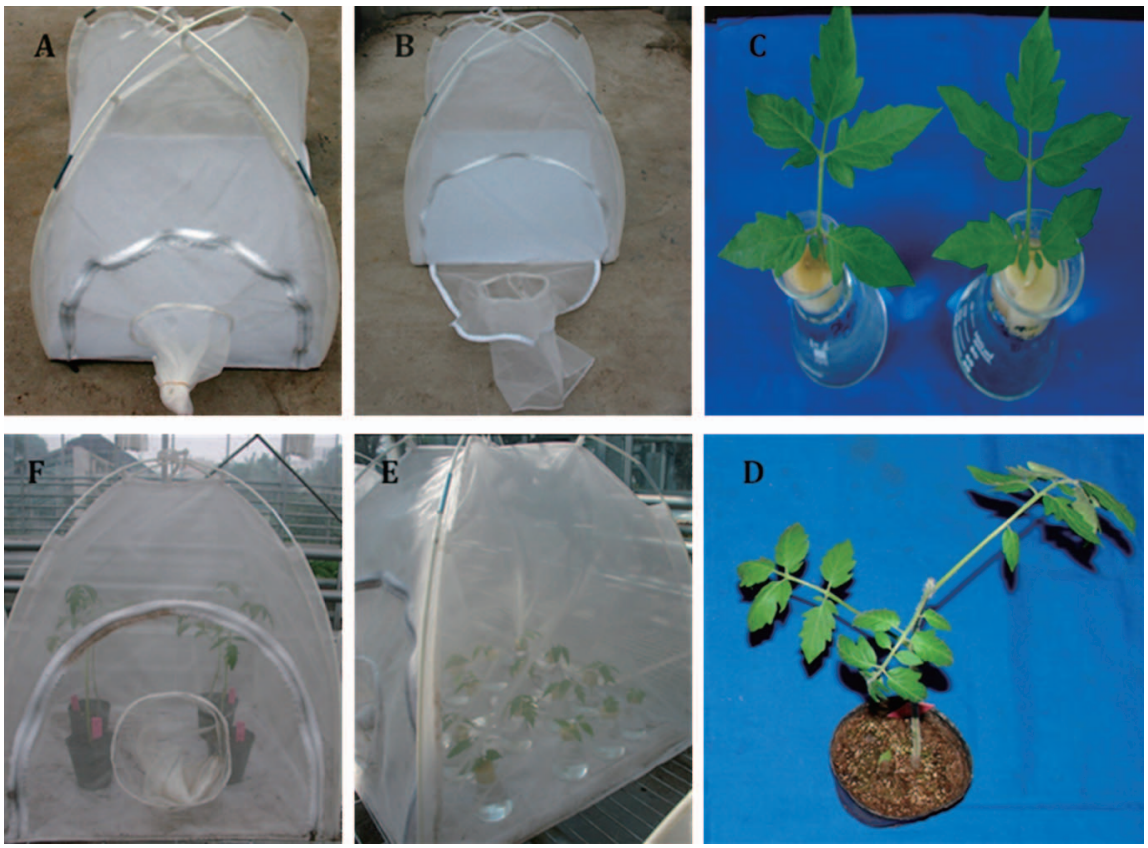

Fig. 3. Plant materials and cages *in vivo* bioassay and *in vitro* bioassay. A. cage closed; B. open; C. leaves prepared for *in vitro* bioassays; D. plant ready for *in vivo* bioassay; E. leaves in a cage; F. plants in a cage.

Leaves and plants were taken out of the cages at two, four, six and eight hours (four replications). Care was exercised so that adult whiteflies remained inside the cage during these sampling periods. Every leaflet was observed under a stereomicroscope (×50, Stemi 2000C, ZEISS) and the number of eggs on the abaxial surface was counted. After counting eggs, leaves and plants were returned to the cages and were not watered until die, in order to kill these whitefly adults and eggs.

Whitefly oviposition on different tomato genotypes

The five tomato genotypes mentioned previously were raised to so that leaves at nodes 2–4 were sufficiently developed for testing. Four intact plants and eight excised leaves of each genotype were placed in cages and infested as described previously. Leaves and plants were removed from the cages after eight hours and the numbers of eggs on the abaxial surfaces were counted as described above.

Data analysis

Data on eggs/per leaflet were used to determine oviposition rate. Log transformation was used to normalize oviposition rate data. The formula of the transformation is Log10 (eggs/per leaflet + 0.5). Standardized data were subjected to ANOVA and LSmeans were compared using the least significant difference in different levels ($P = 0.05, 0.01$).

Results

Whitefly oviposition at different leaf nodes and different times

Test was not a significant source of variation, meaning that there was no difference between *in vitro* test and *in vivo* test. As expected, leaf node and sampling time were the most significant sources of variation for whitefly eggs/per leaflet. All other sources of variation in whitefly eggs/per leaflet were associated with leaf node and sampling time (Table 1).

The cultivar 9706 genotype was evaluated with *in vitro* and *in vivo* bioassays. Eggs/per leaflet were greatest on the 2nd leaf. Eggs/per leaflet on the 3rd leaf were greater than on the 4th leaf. Eggs/per leaflet on the 2nd leaf and on the 3rd leaf were significant difference with on the 4th leaf ($F = 24.57$, $P < 0.0001$, Table 1), indicating that whiteflies exhibited the greater preference for oviposition on the younger leaf (Table 2). Eggs/per leaflet generally increased over time of exposure, with maximum numbers at 8 hours. Eggs/per leaflet were significant difference between different sampling times ($F = 18.70$, $P < 0.0001$, Table 1) (Table 2).

When individual leaves of cultivar 9706 genotype were evaluated with *in vitro* test, eggs/per leaflet were greatest on the 2nd leaf, and were significant difference between different leaf nodes (Table 2). *In vivo* test eggs/per leaflet were greatest on the 3rd leaf. Eggs/per leaflet on the 2nd leaf were

Table 1. Sums of squares and F values from repeated measures analysis of variance of the Log10 (eggs/per leaflet + 0.5) on abaxial surfaces of cultivar 9706 tomato leaves in *in vitro* test and in *in vivo* test

Source of variation	Log10 (Eggs/per leaflet + 0.5)				
	df	Type III SS[a]	Mean Square	F Value	Pr > F
Test (T)	1	0.69369604	0.69369604	3.62[NS]	0.0576
Leaf Node (LN)	2	9.40760283	4.70380141	24.57**	<.0001
Sampling Time (ST)	3	7.15818327	3.57909163	18.70**	<.0001
T*LN	2	15.39339755	5.13113252	26.80**	<.0001
T*ST	3	1.52070129	0.50690043	2.65*	0.0485
LN*ST	6	3.26222147	0.54370358	2.84*	0.0100
T*LN*ST	6	2.48068554	0.41344759	2.16*	0.0458

[a] Sums of squares.
[NS],*,** No significant (NS) at the 5% or Significant at the 5% (*) or 1% (**) levels.
The CV was 36.9% in the experiment.

Table 2. LSmeans (±SE) of whitefly Log10 (eggs/per leaflet + 0.5) on abaxial surfaces of cultivar 9706 tomato leaves evaluated at sources of variation *in vitro* bioassay and *in vivo* bioassay

Source of variance (Log10 (Eggs/per leaflet + 0.5) LSMEANS ± Standard Error)[a]									
Leaf Node (LN)		Sampling Time(ST)		Test*Leaf Node (T*LN)			Test*Sampling Time (T*ST)		
2nd leaf	1.29 ± 0.03 A	2 (h)	0.96 ± 0.04 D		2nd leaf	1.43 ± 0.05 A		2 (h)	0.94 ± 0.06 C
3rd leaf	1.27 ± 0.04 A	4 (h)	1.11 ± 0.04 C	*In vitro*	3rd leaf	1.14 ± 0.05 B	*In vitro*	4 (h)	1.15 ± 0.06 C
4th leaf	0.99±0.03 B	6 (h)	1.22 ± 0.04 B		4th leaf	0.87 ± 0.05 C		6 (h)	1.13 ± 0.06 C
		8 (h)	1.45 ± 0.04 A		2nd leaf	1.16 ± 0.05 B		8 (h)	1.37 ± 0.06 B
				In vivo	3rd leaf	1.40 ± 0.05 A		2 (h)	0.97 ± 0.06 C
					4th leaf	1.11 ± 0.05 B	*In vivo*	4 (h)	1.06 ± 0.06 C
								6 (h)	1.32 ± 0.06 B
								8 (h)	1.54 ± 0.56 A

LSMEANS means least squares means.
[a] Within each column, LSMEANS followed the same letter do not differ at the 5% level of significance, as determined by LSD of the adjusted means.

Table 3. Sums of squares and F values from repeated measures analysis of variance of the Log10 (eggs/per leaflet + 0.5) on abaxial surfaces of five tomato genotypes *in vitro* bioassay and *in vivo* bioassay

Source of variance	Log10 (Eggs/per leaflet + 0.5)				
	df	Type III SS[a]	Mean Square	F Value	Pr > F
Test (T)	1	0.04129116	0.04129116	0.17 [NS]	0.6822
Leaf Node (LN)	1	4.68295868	4.68295868	19.03**	<.0001
Genotypes (G)	4	41.05360568	10.26340142	41.71**	<.0001
T*LN	1	0.39337691	0.39337691	1.60 [NS]	0.2066
T*G	4	4.59889263	1.14972316	4.67**	0.0010
LN*G	4	1.53567359	0.38391840	1.56 [NS]	0.1834
T*LN*G	4	1.40562593	0.35140648	1.43 [NS]	0.2231

[a] Sums of squares.
[NS],*,** No significant (NS) or Significant at the 5% (*) or 1% (**) levels.

greater than on the 4th leaf, but there were no significant difference between them (Table 2).

In vitro test and *in vivo* test, eggs/per leaflet were increased following the extensions of sampling time, with maximum numbers at 8 hours. Eggs/per leaflet at 8 hours *in vivo* test were greater than *in vitro* test and were significant difference between them. Eggs/per leaflet at 8 hours *in vitro* test were no significant difference with at 6 hours *in vivo* test, indicating that whiteflies *in vivo* test had higher oviposition rate than *in vitro* test (Table 2).

Whitefly oviposition on different tomato genotypes

As the above result, test was not a significant source of variation for eggs/per leaflet on different tomato genotypes, indicating that there were the same results between *in vitro* test and *in vivo* test. Genotypes and leaf node were significant sources of variation for eggs/per leaflet. The only other significant source of variation was test*genotype interaction (Table 3).

Younger leaf 2nd leaf and 3rd leaf were chose on different tomato genotypes for whitefly resistance. The result was

Table 4. LSmeans (±SE) of whitefly Log10 (eggs/per leaflet + 0.5) on abaxial surfaces of leaves of five tomato genotypes evaluated at sources of variation *in vitro* bioassay and *in vivo* bioassay

Source of variance (Log10 (Eggs/per leaflet + 0.5) LSMEANS ± Standard Error)[a]						
Leaf Nodes (LN)		Genotype (G)		Test*Genotype (T*G)		
2nd leaf	0.33 ± 0.03 B	cultivar 9706	0.60 ± 0.05 A	*In vitro*	cultivar 9706	0.59 ± 0.06 A
3rd leaf	0.50 ± 0.03 A	Zaofen2	0.64 ± 0.05 A		Zaofen2	0.63 ± 0.06 A
		Moneymaker	0.65 ± 0.05 A		Moneymaker	0.73 ± 0.06 A
		LA1777	0.09 ± 0.05 B		LA1777	0.16 ± 0.06 B
		PI134417	0.10 ± 0.05 B		PI134417	–0.07 ± 0.06 B
				In vivo	cultivar 9706	0.61 ± 0.06 A
					Zaofen2	0.65 ± 0.06 A
					Moneymaker	0.57 ± 0.06 A
					LA1777	0.03 ± 0.06 B
					PI134417	0.26 ± 0.06 B

LSMEANS means least squares means.

[a] Within each column, LSMEANS followed the same letter do not differ at the 5% level of significance, as determined by LSD of the adjusted means.

different with on the susceptible cultivated tomato cultivar 9706. Eggs/per leaflet on the 3rd leaf were greater than on the 2nd leaf, and were significant difference between them ($F = 19.03$, $P < 0.001$, Tables 3, 4). As expected, eggs/per leaflet on the cultivated tomatoes were greater than on the wild tomatoes, and were significant difference between them ($F = 41.71$, $P < 0.0001$, Table 3). There were no differences among the three cultivated tomatoes and between the two wild tomatoes (Table 4).

Whitefly had different oviposition preferences on the wild and cultivated tomatoes as shown by experiments *in vitro* test and *in vivo* test. Whiteflies laid significantly fewer eggs on the 2nd and 3rd leaves of the wild species than on the cultivars ($F = 4.67$, $P < 0.01$, Table 3). *In vitro* test, eggs/per leaflet were the most on Moneymaker cultivar and were the least on PI134417 genotype. *In vivo* test, eggs/per leaflet were the most on Zaofen 2 cultivar and were the least on LA1777 genotype. But *in vitro* test and *in vivo* test, there were no difference between cultivated tomatoes and between wild tomatoes, indicating that *in vitro* test and *in vivo* test had the same effect for evaluating whitefly oviposition rate (Table 4).

Discussion

Most studies have shown that whitefly prefer to oviposit on younger leaves. The results supported this viewpoint. Whiteflies showed the greatest preference for oviposition on the 2nd leaf for tomato leaves evaluated *in vitro*. For plants evaluated *in vivo*, they preferred the 3rd leaf. They exhibited the least preference for the 4th leaf of *in vitro* leaves (Table 2). Young leaves were more susceptible to whitefly oviposition than old leaves in the *in vitro* tests of cultivar 9706. This observation is in accordance with finding reporting higher oviposition rates on leaves having dense trichomes positioned close to the stem terminus (Heinz and Zalom 1995). In free choice tests, whiteflies laid significantly more eggs on the hirsute and pubescent isolines of soybean, than on a glabrous isoline (McAUSLANE 1996). In other free choice tests, 20 day old cotton seedlings were preferred for oviposition in populations of 100 to 150 adults per plant (Campos *et al.* 2005). Whiteflies have previously been shown to prefer younger leaves to older leaves for oviposition, although this preference was overridden by changing normal leaf position (Liu and Stansly 1995). Perhaps this explains why eggs were greater in number on the 3rd than on the 2nd leaf in the *in vivo* tests (Table 2). Leaf positioning in space was thus a factor affecting whitefly oviposition. This problem can be avoided by testing for whitefly resistance using *in vitro* tests in which all leaves, regardless of their developmental position are tested at the same height within the cage. Plant developmental stage is thus a factor affecting whitefly oviposition. We consequently focused next, on the resistance to whitefly of the young leaves of differing tomato genotypes.

Infestation time and number of whitefly adults are factors affecting oviposition. For example, two whitefly females were placed in small cages for 4 days before observing oviposition (Nombela *et al.* 2000). Twenty whitefly females were placed in a small cage for 24 hours (Muigai *et al.* 2002). Ten whitefly females were placed in a small cage for 24 hours (Momotaz *et al.* 2010). As we used 100 whitefly adults per leaf, we reduced the measurement times to 2, 4, 6 and 8 hours. We found that egg numbers generally increased as time extension; by 8 hours there were significant differences among genotypes for the *in vitro* tests. We therefore chose 8 hours as the most suitable time to measure oviposition rate.

High levels of resistance to whitefly have been observed for *S. habrochaites* and *S. pennellii* (Heinz and Zalom 1995). *S. habrochaites* has been reported to have a high level of resistance to four insects including whitefly (Carter *et al.* 1989, Channarayappa *et al.* 1992, Eigenbrode and Trumble 1993, Juvik *et al.* 1982, Schuster 1998). *S. habrochaites* exhibited high levels of whitefly resistance in a greenhouse bioassay (Muigai *et al.* 2003). *S. habrochaites* strains (LA1777, PI134417) contain volatile organic compounds

(Fridman *et al.* 2005) that have shown high levels of repellent and fumigant activity against adult whitefly (Muigai *et al.* 2002). Our conclusion was similar. Wild tomatoes had fewer whitefly eggs than cultivars, in both *in vitro* and *in vivo* experiments. *In vitro* test and *in vivo* test, eggs/per leaflet were different on the same genotype tomatoes, but were no significant difference between them (Table 4). Genotype was the greatest source of variation and test was not the source of variation (Table 3), indicating that *in vitro* test and *in vivo* test had the same effect for evaluating whitefly oviposition rate. Firdaus *et al.* (2012) reported leaf disc tests were an alternative *in vitro* method that can be used for whitefly resistance screening. Our result supported that *in vitro* test was a good alternative for evaluating whitefly resistance.

Our method of assessing whitefly resistance using tests of leaves held *in vitro* has some advantages over earlier *in vivo* methods. It takes only one or two days, requires only a small space and is appropriate for testing the resistance of large plant populations. As plants can continue to grow it is a simple operation with strong repeatability for some temporary populations (e.g. BC_1, F_2). As all leaves are the same height the use of *in vitro* test can avoid the influence of leaf position in space on whitefly oviposition. After testing, plants can be transplanted and allowed to set seed and whiteflies for testing can be killed easily in cages. This point is very important in China. There are no related measures for controlling whiteflies which are used in experiments. So the whiteflies for testing are major sources of threatening whiteflies in agricultural crops. This *in vitro* method is used to solve the problem of whiteflies elimination. Compared with the earlier *in vitro* method (Firdaus *et al.* 2012), our *in vitro* method is more economize and more convenience. Because we use big cages instead of small cages, and uses water instead of medium to keep leaves fresh. So this method is appropriate for breeders who have big populations or have not so much money. This *in vitro* method may be further refined and explored in future, for the evaluation of whitefly resistance in tomato.

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